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1 **Camouflage accuracy in Sahara-Sahel desert rodents**

2

3 **Authors:**

4 Ossi Nokelainen^{1*}, José Carlos Brito², Nicholas E. Scott-Samuel³, Janne K.

5 Valkonen¹ & Zbyszek Boratyński²

6

7 **Addresses:**

8 ¹Department of Biological and Environmental Science, University of Jyväskylä, P.O.

9 Box 35, 40014 University of Jyväskylä, Finland

10 ²CIBIO-InBIO Associate Laboratory, Research Center in Biodiversity and Genetic

11 Resources, University of Porto, Vairão, 4485-661, Portugal

12 ³School of Psychological Science, University of Bristol, Bristol, UK

13 * Author for correspondence (ossi.nokelainen@jyu.fi)

14

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17

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19 Background matching, desert, *Gerbillinae*, *Dipodinae*, top-down selection, vision

20 model, QCPA

21 ABSTRACT

22 1. Camouflage helps animals to hide from predators and is therefore key to survival.

23 Although widespread convergence of animal phenotypes to their natural
24 environment is well established, there is a lack of knowledge about how species
25 compromise camouflage accuracy across different background types in their habitat.

26 2. Here we tested how background matching has responded to top-down selection by
27 avian and mammalian predators using Sahara-Sahel desert rodents in North Africa.

28 3. We show that the fur coloration of several species has become an accurate match to
29 different types of desert habitats. This is supported by a correlation analysis of colour
30 and pattern metrics, investigation of animal-to-background similarities at different
31 spatial scales, and is confirmed by modelling of two predator vision systems.

32 4. The background match was closest across large (or global) spatial scales, suggesting
33 a generalist camouflage tactic for many background types. Some species, may have
34 a better match to the background over small (or focal) spatial scales, which could be
35 the result of habitat choices or differential predation. Nevertheless, predicted
36 discrimination distances of fur coloration were virtually indistinguishable for
37 mammalian and low for avian vision model, which implies effective camouflage.

38 5. Our study provides one of the best documented cases of multilevel camouflage
39 accuracy in geographically widespread taxa. We conclude that background matching
40 has become an effective and common adaptation against predatory threat in Sahara-
41 Sahelian desert rodents.

42 INTRODUCTION

43 Camouflage is a widespread anti-predator adaptation that hinders detection or
44 recognition by increasing prey resemblance to natural environment or objects therein
45 (Poulton 1890, Cott 1940, Endler 1980, Bond and Kamil 2002, Ruxton et al. 2004,
46 Stevens and Merilaita 2011, Troscianko et al. 2013, Hultgren and Mittelstaed 2015,
47 Duarte et al. 2018, Nokelainen et al. 2019). As the adaptive value of camouflage most
48 commonly relies upon the similarity of individuals to visual features of the
49 environment, specific phenotypic characteristics should only be effective in a limited
50 set of environments (Thayer 1896, Cott 1940, Ruxton et al. 2004, Stevens and Merilaita
51 2009, Hughes et al. 2019). Hence, the use of certain coloration across varied
52 environments, where effective concealment requires matching different types of
53 lightness (i.e. the reflected light intensity or brightness), colour and pattern elements,
54 should constrain the location and/or habitat use of a given species: they will be safest
55 in a single habitat, or multiple similar habitats.

56 Animals have many ways to optimise camouflage. For example, they may
57 evolve a generalist tactic, which confers a reasonable level of concealment across a
58 range of habitat types but fails to be optimal in any one (Merilaita et al. 1999, Houston
59 et al. 2007). This can be viewed as ‘imperfect camouflage’, a compromise to match
60 different visual backgrounds (Hughes et al. 2019). Alternatively, they may adopt more
61 specialised camouflage, which provides better protection in certain environments but
62 constrains the use of other habitats at the cost of increased vulnerability (Merilaita et
63 al. 1999, 2001, Kjernsmo and Merilaita 2012, Michalis et al. 2017). Thus, it can be
64 predicted that animals which range over heterogenous environments, e.g. those with
65 large distributions, high mobility or migratory behaviour, should adopt a more
66 generalist and/or compromise camouflage tactic. In contrast, less mobile, sedentary

species and less strong competitors should rely on more specialised camouflage (Merilaita et al. 2017, Fennell et al. 2018, Hughes et al. 2019). The same may also be true of polymorphic species where different morphotypes thrive in those respective habitat patches that offer the best concealment (Hoekstra et al. 2009, Cook et al. 2012, Karpestam et al. 2013). Although convergence of phenotype-environment features is well-known from classical works (Thayer 1896, Cott 1940, Cain and Sheppard 1954) and now quantified across several taxa (e.g. cuttlefish, Barbosa et al. 2008; geometrid moths, Kang et al. 2012; ground-nesting birds, Wilson-Aggarwal et al. 2016), direct demonstrations of camouflage have traditionally been scarce. This is because quantifying camouflage whilst controlling for different natural background types is challenging, and because suitable tools have only recently become widely available. Hence, a state-of-the-art demonstration would allow understanding of how camouflage is optimised and whether generalist or specialist tactics prevail (Rosenblum 2006, Troscianko et al. 2016, Wilson-Aggarwal et al. 2016).

Desert rodent communities present an excellent opportunity to study how background matching is optimised in the wild. For instance, desert rodents of the Sahara-Sahel biogeographic region have repeatedly evolved variable levels of background matching: phenotypic variation of fur coloration that resembles different background types, measured over a large spatial scale (Boratyński et al. 2017). The desert rodent species are expected to have variable home ranges and mobility, and thus may face different requirements for efficient camouflage (Fig. 1). Furthermore, living in open habitats (i.e. lacking overarching tree canopy and continuous bush vegetation) makes these rodents particularly exposed to predator driven (or top-down) selection. The chief reason for desert rodent coloration is thought to be camouflage against visually-guided predators (Boratyński et al. 2014, 2017). To support this, a detailed

analysis of background match is required. In the case of desert rodents, previous work has not taken into account variation in visual background for camouflage, and has not analysed camouflage from the predator perspective (e.g. using vision models). Importantly, as fur coloration in rodents is variable and a heritable trait underpinned by substantial genetic mechanisms (Nachman et al. 2003, Mullen et al. 2009, Hubbard et al. 2010), camouflage can be a good marker of selection, alternative tactics and adaptation (Caro et al. 2017, Cuthill et al. 2017).

We ask whether coloration of desert rodents has become an accurate match to the diverse habitats they live in. More specifically, we study their background matching tactics by comparing dorsal fur coloration of several species with different habitat types. We test how well these animals match their focal habitat (i.e. the specific background from which the animal was found - a small scale microhabitat) in relation to the global habitat (i.e. all backgrounds that the species utilizes - a large-scale macrohabitat) and link the similarity to background with their evolutionary history. Finally, we use visual modelling of two available visual systems to test whether phenotypic variation mirror substrate-specific camouflage against visually-guided predators.

We test the following hypotheses. 1) If top-down predator selection has driven background matching of animal coloration, colour and pattern metrics of dorsal fur should positively correlate with those of the backgrounds. 2) If animals are able to seek backgrounds against which they are harder to find (Kang et al. 2012, Duarte et al. 2016, Marshall et al. 2016, van Bergen and Beldade 2019), then the camouflage match should be best on the (focal) background where the animal is found. Alternatively, if species are adapted to match a broader range of environments (Merilaita et al. 2017, Michalis et al. 2017, Hughes et al. 2019), then animals may better match several available (global) background types that the species commonly uses. We also predict that over

the course of their evolutionary history the species should have evolved an effective background match (Boratyński et al. 2017). 3) The similarity to the background should be hard to distinguish when viewed through predator vision systems (Endler 1978, Kelber et al. 2003, Nokelainen et al. 2017, Maia and White 2018). Here we focus on two predator types, mammals and birds, because rodents are key prey for both (Bleicher et al. 2016, 2018, Kotler et al. 2016). We expect that the vision model predicted animal-to-background discrimination contrasts will be near to perceptible (Endler 1978, Cloudsley-Thompson 1999, Maia and White 2018). Applying this unique combination of tests on prey community allows a more complete understanding of how camouflage is optimised in wild animal populations.

MATERIALS AND METHODS

Animals and their phenotypes

Expeditions were organized to the Sahara-Sahel parts of Mauritania and Morocco (Brito et al. 2011, Boratyński et al. 2013, Moutinho et al. 2015, Guerreiro et al. 2016). Specimen capture was performed with minimum invasive methods, using life-traps (Sherman, Folding Aluminum Heavy Duty) and hand-held nets (when searching for active animals at night). Altogether, 163 animals were obtained for analysis (Fig. 2A): 29 *Gerbillus amoenus*, 29 *Gerbillus gerbillus*, 33 *Gerbillus tarabuli*, 53 *Jaculus hirtipes*, 3 *Meriones libycus*, 8 *Pachyuromys duprasi*, and 8 *Psammomys obesus*.

In order to quantify phenotypes and their match to the background, we photographed both the animals and their habitat backgrounds. All animals were photographed out in the field. In each case, we focused on the entire animal dorsal view (excluding tail) and their respective backgrounds. Photographs were mostly taken at dark and frame was supplemented using white led torch. No light diffusor was used;

although, care was taken so that light would fall similarly on the scene. Photographs were taken from similar height (ca. 1 meter). However, a known scale (a colour standard with a millimeter ruler) was included in the photographic scene for further analysis.

Photographs were taken with a Canon EOS 400D digital camera with a Canon 18–55mm kit lens. The images were saved in RAW format with manual white balance. During calibration in Image J (Troschianko and Stevens 2015) images were converted to uncompressed TIFF files, and the images of each animal comprised three bandpass layers corresponding to the long-wavelength (LW), medium-wavelength (MW), and short-wavelength (SW) parts of the visible spectrum. Due to logistical constraints we were not able to include UV in our analysis; however, as the analysed species are crepuscular or nocturnal the UV reflectance was expected to be unimportant. On the other hand, as many of these animals are active during dusk and dawn, colour vision may be used by both predator or prey. Differences in ambient light were controlled by standardizing (equalizing) the images to a grey standard (X-Rite Classic, corresponding to equal reflectance at white, black and 18% grey), and scaling each image channel to reflectance, where an image value of 255 on an 8-bit scale equals 100% reflectance (Stevens et al. 2007, Troschianko and Stevens 2015).

Pattern analysis

The pattern analyses technique (i.e. granularity analysis) involves decomposing an image into a series of different spatial frequencies using Fourier analysis and band pass filtering, followed by determining the relative contribution of different marking sizes to the overall pattern (Barbosa et al. 2008, Hanlon et al. 2009, Stoddard and Stevens 2010). We used this technique to investigate whether rodent coloration with respect to the pattern corresponds to that of backgrounds. Noteworthy, pattern analysis does not

directly measure pattern similarity but rather pattern features. Therefore, we conducted a correlation analysis to compare pattern features between the animal and the background. In further analysis (i.e. similarity to background and vision modelling), however, phase information was ignored, as the patterns analysed were not rich in distinctive spatial features and could therefore be approximated as uniform textures.

Pattern analysis was conducted in custom files for Image J (Troschianko and Stevens 2015), with analysis based on different pixel sizes (or spatial filter). The analysis calculates the amount of information (or pixel energy) corresponding to markings of different sizes, starting with small markings (we used a pixel start size of 2) and increasing in size to larger markings (we used a pixel end size of 250). Increase in pixel step size was set to multiply each step by 1.414, thus representing exponential growth. The luminance was measured over 20 bands from lowest luminance (0) to highest luminance (65535), the maximum dynamic range of a 32-bit tiff image. The luminance channel was set to double cones for the avian vision model and rods for the mammalian vision model (see more details below). As a resulting information, from each image we obtained texture information as marking size (i.e. the spatial frequency with the highest pixel energy), pattern dominance (i.e. maximum energy – the energy at the spatial frequency with the highest pixel energy), pattern diversity (i.e. proportional power – maximum or peak energy value divided by the summed energy), and contrast (i.e. total power or amplitude – the energy summed across all scales).

Animals' similarity to background

To investigate whether rodents are found against backgrounds where they maximise similarity to background, we used two approaches. First, to illustrate the spread of the colour values in animals and backgrounds, we converted normalised camera responses

(i.e. raw RGB-values) to two-dimensional XY-colour space (Fig. 2B, ESM Table S1). The conversion was done with previously used methods (Kelber et al. 2003, Nokelainen et al. 2018; ESM Table S1). Animal-to-background distances using Euclidian distances in XY-coordinate space were generally very low (range = 0.01 – 0.19, mean = 0.03, s.d. = 0.03) indicating very accurate background match albeit the spread in background variation (ESM Table S3, ESM Fig. 1-2).

Next, we investigated the animals' similarity to the background with respect to focal and global habitats (Fig. 2C). 'Focal' refers to the specific background from which the animal was found (i.e. representing small scale microhabitat), and 'global' refers to all backgrounds that other members of the same species were found in (i.e. representing larger-scale macrohabitat). This restricts the 'global habitat' definition to within-species. To quantify the 'similarity to background', we used an extension of the multispectral imaging tool box in image J (Troschianko and Stevens 2015): Quantitative Colour and Pattern Analysis framework (Van Den Berg et al. 2019). We used 'colour map' approach (with default settings) that analyses the similarity of the regions of interest from images (e.g. the animal and the background). The method utilizes the camera's colour channel information to plot the overlap of the specified regions in colour space (Van Den Berg et al. 2019). We used photographs modelled to human cone catch images (Canon 400D 18 to 55mm D65 to Human D65) and acuity uncorrected maps. The similarity to background is described as non-parametric index, a relative value ranging from 0 to 1 (i.e. 0 overlap equals to no overlap in chromatic space whereas 1 equal to 100% similarity).

Visual modelling camouflage accuracy

Visual modelling, initial image calibration and analysis followed previously described methods (Stevens et al. 2007, Troscianko and Stevens 2015, Van Den Berg et al. 2019), which have proven effective in quantifying camouflage (Nokelainen et al. 2017, 2018, Stevens et al. 2017). To examine how visible desert rodents were for predator perception, we used a receptor-noise limited visual discrimination model (Vorobyev et al. 1998). We used mammalian (ferret) and avian (peafowl) vision model proxies, because the visual systems of these ‘vision model organisms’ are well characterised. For both, we used a conservative 0.1 Weber fraction for luminance contrast. However, using different Weber values (e.g. 0.05) for luminance gave qualitatively similar results. For luminance contrast calculations we used double cones for avian vision model and rod receptors for the mammalian vision model. For the chromatic contrast of the mammalian visual model (i.e. ferret), we used Weber fractions SW 0.187, LW 0.050 with receptor ratio 1:14, respectively (Calderone and Jacobs 2003). For the avian visual model (i.e. peafowl), we used Weber fractions SW 0.053, MW 0.050, LW 0.051 with receptor ratio 1.9:2.2:2.1, respectively (Hart 2002). The avian visual model was used over the 400–700 nm range (as in Kang et al. 2015), as UV data were not available. However, we may assume the significance of UV to be negligible in the typical viewing conditions during dawn or dusk. As end product, the vision model yields values in ‘just noticeable differences’ (JNDs). Values lower than one (<1 JND) are indistinguishable, whereas larger values are increasingly likely to be discriminable (Siddiqi et al. 2004, Kang et al. 2015, Nokelainen et al. 2019). For visual modelling we used six species, omitting *Meriones libycus* due to small sample size ($n = 3$), for cross-background comparisons. The results were plotted against four subjectively different habitat classes: clay ($n = 44$), sand ($n = 78$), gravel ($n = 18$) and rock ($n = 8$) habitats (fifteen cases were unclassified and not included in the analysis).

241

242 Statistical analyses

243 To investigate whether colour and pattern metrics of animals positively correlate with
244 those of the backgrounds, we first investigated the colour metrics with Pearson
245 correlation index and with descriptive statistics: range, mean and standard deviation.

246 To test whether desert rodents were more often found in habitats where they
247 maximise their similarity to background, we set animal-to-background similarity (S) as
248 the response variable in a linear mixed effects model (lmer-function) in lmerTest R-
249 package (Kuznetsova et al. 2017). Species, background comparison (focal vs. global)
250 and their interaction were set as predictors. Individual was set as random factor to
251 control for data structure. The significance of the factors included in the model was
252 tested using F-test ratios or analysis of variance (or ANOVA).

253 To test whether camouflage effectiveness varies relative to different predator
254 perception, we used three-way repeated measures ANOVA. Essentially, comparisons
255 between two vision models are repeated measures, because after each rodent was
256 photographed its colour values were derived twice for each individual, once for
257 mammalian and once for avian visual systems (as the values were from the same
258 multispectral image, the animal ID was set repeated argument in the model). In the
259 visual model analyses two models were ran, whereby chromatic and luminance JNDs
260 were used as dependent values separately. Of the predictor variables *vision* refers to
261 visual model (mammalian, avian), *species* to the taxonomic group, and *habitat* to the
262 predominant habitat type. Full factorial models were tested and reduced by backward-
263 stepwise model simplification removal of non-significant terms. Analyses were
264 conducted using IBM SPSS Statistics (v22), and program R (3.2.1).

265

RESULTS

Colour and pattern correlations

The comparisons of fur coloration of 163 animals and their backgrounds showed consistent similarity (Fig. 1 exemplifies animal-to-background resemblance). A positive correlation was found for colour characteristics of lightness [$\bar{x}_{\text{animal-background}}$ (s.d.) = 42.035–46.250 (8.844–8.326); $r = 0.256$, $p = 0.001$], LW [i.e. red; $\bar{x}_{\text{animal-background}}$ (s.d.) = 57.425–65.840 (12.803–11.674); $r = 0.333$, $p < 0.001$] and MW reflectance bands [i.e. green; $\bar{x}_{\text{animal-background}}$ (s.d.) = 40.003–43.033 (8.544–8.139); $r = 0.244$, $p = 0.002$], but not for SW [i.e. blue; $\bar{x}_{\text{animal-background}}$ (s.d.) = 28.678–29.876 (6.418–6.545); $r = 0.136$, $p = 0.083$]. Examination of pattern characteristics revealed that pattern dominance [$\bar{x}_{\text{animal-background}}$ (s.d.) = 603.795–429.940 (247.697–150.224); $r = 0.344$, $p < 0.001$] and contrast [$\bar{x}_{\text{animal-background}}$ (s.d.) = 5897.116–4118.650 (1687.779–1462.082); $r = 0.255$, $p = 0.001$] between fur and background were correlated, whereas marking size [$\bar{x}_{\text{animal-background}}$ (s.d.) = 91.217–11.544 (54.558–30.456); $r = -0.090$, $p = 0.250$] and pattern diversity [$\bar{x}_{\text{animal-background}}$ (s.d.) = 0.085–0.085 (0.008–0.009); $r = -0.026$, $p = 0.738$] were not (ESM Table S2).

Investigation of XY-colour coordinates revealed that species that were found from habitats with a wider range of spread in colour coordinates (e.g. *Gerbillus gerbillus*, *G. tarabuli*, *Jaculus hirtipes*), also had a similar range and standard deviations of fur colour with respect to backgrounds (Table 1). In comparison, species inhabiting more homogeneous habitats in terms XY-colour coordinates (e.g. *Gerbillus amoneus* and *Psammomys obesus*) showed narrower spread in fur colour (Fig. 2A-B).

Animal-to-background similarity

To assess whether the camouflage match was best against the background where the animal was found, we compared fur coloration between the ‘focal’ microhabitat and ‘global’ macrohabitat (Fig. 2C, Table 2). The similarity to background values were higher at ‘global’ level supporting a generalist camouflage strategy for most species (comparison by species interaction, ANOVA $F_{6,151} = 3.010$, $p = 0.008$). There were considerable differences in the overall similarity to background between species (min = 0.014, median = 0.578, max = 0.899). The most similar animal to background was *P. obesus* (median = 0.77, s.d. = 0.12), followed by *G. tarabuli* (median = 0.72, s.d. = 0.14), *G. gerbillus* (median = 0.65, s.d. = 0.20), *G. amoneus* (median = 0.62, s.d. = 0.15), *P. duprasi* (median = 0.55, s.d. = 0.18), *M. libycus* (median = 0.37, s.d. = 0.15), whereas the least similar to background was *J. hirtipes* (median = 0.34, s.d. = 0.19). Interestingly, more recently diverged species showed an apparent match to the background (Fig. 2D).

Vision modelling camouflage accuracy

Fur coloration was a very accurate match to several types of backgrounds, as confirmed by the visual modelling results for both avian and mammalian perception (Fig.3). Results showed a three-way interaction in luminance contrasts, indicating that desert rodent species have different perceived luminance against various types of natural backgrounds and predator visual systems (Table 3). *Gerbillus amoneus* had the highest luminance contrasts in comparison to other species, and its contrast was especially high against sand habitat. However, *G. gerbillus* had low contrast values against the sand and rock backgrounds for the avian vision model, and for mammalian vision model its luminance contrast was even lower against rocks but higher against sand.

Chromatic contrast values showed an interaction between vision model used and rodent species (Table 3). Colour discrimination values of fur colour were virtually indistinguishable ('just noticeable differences', $JND < 1$) for the mammalian vision model, and generally low ($JND = 1 - 4$) for the avian vision model. For both visual models, chromatic (colour) discrimination values between fur and background were lower than luminance values (Table 3, Fig. 3). Luminance contrast values for both visual models ranged between < 1 and < 10 , depending on the species and habitat. Nevertheless, all desert rodent species tested here possessed very accurate colour camouflage (typically < 3 JNDs) on varied backgrounds (Fig. 3).

DISCUSSION

Camouflage accuracy in Sahara-Sahelian rodents presents a remarkably fine-tuned example of background matching, spanning over a large biogeographic zone. Both the colour and pattern of animals were correlated with their corresponding background values. Animal-to-background similarity was generally high at global scale, supporting a generalist camouflage tactic for most species tested here. The colour match was excellent in terms of a mammalian vision model, and analyses also suggested effective concealment from avian vision model. Our findings highlight one of the best documented cases of phenotype-environment convergence in geographically widespread species complex.

We predicted that if top-down predator selection has driven background matching in desert rodent coloration, animal colour and pattern metrics should correlate with corresponding values of backgrounds. Previous research, using remote sensing and digital image data, showed that RGB-values of desert rodents fur match large spatial scales (at 10 and 1 km radius) of the background environment RGB-values

(Boratyński et al. 2014, 2017). Our results support these findings: rodents match the background of habitats they use in terms of not only colour, but also pattern dominance and contrast. The pattern match may also be important for camouflage because natural environments are variable in visual texture (Michalis et al. 2017), such as substrate granule size (for example, riverbanks and dried river, wadis, harbour variable sized gravel, rocks and pebbles). This sets different requirements for species that live in such habitats (Cuthill et al. 2005, Merilaita and Lind 2005, Kjernsmo and Merilaita 2012, Dimitrova and Merilaita 2014). For example, Hughes et al. (2019) have suggested that large-patched details in microhabitat, such as mottled or disjunct backgrounds, should select for specialist forms of camouflage, whereas small-patched details should select for more generalist or compromise camouflage.

Indeed, camouflaged species should show similar spread in colour metrics as their respective habitats. We found that the spread of XY-colour coordinates of animals and backgrounds showed similar ranges, means and standard deviations. Some species (e.g. *G. gerbillus*, *G. tarabuli*, *J. hirtipes*) had higher spread of colour variation as indicated by higher standard deviations, which may indicate more versatile habitat use. Other species utilising more homogeneous habitats at least in terms of XY-colour coordinates, showed narrower spread in coloration (e.g. *Gerbillus amoneus* and *Psammomys obesus*). Together, this implies that species living in more variable habitats may use a greater range of habitats without sacrifices to general resemblance to background (Merilaita et al. 1999, 2001, Kjernsmo and Merilaita 2012, Michalis et al. 2017, Nokelainen et al. 2019).

Predatory threat is known to influence habitat choice in desert rodents (Brown et al. 1988, Kotler et al. 1991, Bleicher et al. 2016, 2018) and some species do behaviourally modulate their camouflage (Kang et al. 2012, 2015, Lovell et al. 2013,

Marshall et al. 2016, Stevens and Ruxton 2019). In contrast, we found that the similarity to the backgrounds was generally better at ‘global’ scale, which supports a general background matching tactic. Judging from the similarity values and vision modelling, camouflage may have evolved to be accurate enough that there is less need for elaborate behaviour to seek specific background types. At the species level, *Psammomys obesus* had the closest similarity to background and impressively at highest their coloration reached 89 per cent similarity to background coloration. At the other end, *Jaculus hirtipes* had poor background match in comparison to other species, potentially because this species is highly mobile and may rely more on speed and manoeuvrability when evading predators (Moore et al. 2017). Nonetheless, some desert rodents may behaviorally improve the match to the background, for instance under dominance competition – although direct demonstration of this requires experimental verification. More generally speaking, it is important to note that in addition to behaviourally adjusting the match to the background (Kang et al. 2012), there are various proximate mechanisms in nature that may improve camouflage efficacy, as for example plastic colour change (Duarte et al. 2016, Eacock et al. 2017) or ontogenetic changes that may indicate transition in life-history tactics (Hultgren and Mittelstaed 2015, Nokelainen et al. 2019). It is also plausible that species-species interactions have shaped the co-evolution of camouflage in desert rodents. Finally, although the colour metrics suggest a close correspondence of similarity-to-background values there was a large variation in them, which raises the question how well the animals are disguised against ecologically relevant predators.

Although the chief assumption for why desert rodents often match their environment is camouflage against visually-guided predators (Brown et al. 1988, Kotler and Brown 1988, Boratyński et al. 2014, 2017, Kotler et al. 2016), previous work has

not modelled predator perception. Thus, this was our final aim. We found fur coloration to be a remarkably accurate match to several types of backgrounds for both avian and mammalian visual systems. Animals were virtually indistinguishable from their backgrounds (< 1 JNDs) for mammalian predators and only slightly more distinguishable (1 - 4 JNDs) for avian predators. This may suggest a top-down selection for camouflage accuracy by predators, as birds and mammals seems to be the most biologically relevant predators for desert rodents (Bleicher et al. 2016, 2018, Kotler et al. 2016). While the avian vision model indicated that birds may find perceiving the animals against the background challenging, the mammalian vision model showed that prey/background discrimination on the basis of colour was virtually impossible, potentially due to lack of LW cone receptors in the mammalian retina (Calderone and Jacobs 2003, Maia and White 2018). Hughes et al. (2019) have suggested that prey with dichromatic predators are likely to have a wider range of possible generalist camouflage than those with more receptors, suggesting that generalist camouflage tactics might be more common when predation by mammals outweighs predation by birds. For both vision models, colour distances between fur and background were lower than luminance distances, which may suggest that colour matching may be more important to avoid predator attention. Luminance information may be more variable under natural light conditions, and thus provides a less reliable cue than colour for predators (Endler 1992, Arenas et al. 2014, Cuthill 2019). However, it is important to note that many rodents are crepuscular or nocturnal, and so future work should investigate vulnerability in low light conditions and the role of prey luminance for predators in these conditions.

CONCLUSIONS

We demonstrate, for the first time at a community level, that several prey species have evolved an accurate background matching against two predator vision systems. Predation, as top-down selection pressure, appears to drive phenotype-environment convergence and a generalist or compromise camouflage tactic that, on average, gives the best survival advantage by accurately resembling rich and variable desert environments. Sahara-Sahelian desert rodents thus exemplify one of the best documented cases of background matching spanning over a large biogeographic zone.

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AUTHOR CONTRIBUTIONS

ON wrote the first draft and conducted the analyses; JB enabled the field work in Sahara; NSS refined the questions and helped writing the manuscript; JV helped with the statistics; ZB coordinated the field work, took the photographs and helped draft the manuscript. We have no conflict of interest to declare. All authors gave approval for publication and agree to be held accountable for the work performed therein.

DATA ACCESSIBILITY

The data is archived (<https://doi.org/10.17011/jyx/dataset/68155>) at the repository of University of Jyväskylä (<https://jyx.jyu.fi>).

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658 **Tables and figures**

659 Table 1: Desert rodent fur colour and background colour variation. Descriptive statistics: range, mean
 660 and standard deviation show the spread of animal and background variation in XY-colour space.

Subject		Animal			Background		
Species	XY	Range	\bar{x}	SD	Range	\bar{x}	SD
<i>Gerbillus</i>	x	0.051	0.110	0.013	0.085	0.011	0.021
<i>amoneus</i>	y	0.047	-0.141	0.013	0.063	-0.140	0.015
<i>Gerbillus</i>	x	0.077	0.122	0.185	0.153	0.135	0.369
<i>gerbillus</i>	y	0.072	-0.156	0.173	0.125	-0.166	0.316
<i>Gerbillus</i>	x	0.927	0.111	0.178	0.076	0.115	0.016
<i>tarabuli</i>	y	0.078	-0.145	0.178	0.082	-0.146	0.017
<i>Jaculus</i>	x	0.076	0.070	0.153	0.080	0.109	0.018
<i>hirtipes</i>	y	0.095	-0.098	0.018	0.078	-0.135	0.017
<i>Meriones</i>	x	0.010	0.085	0.005	0.060	0.141	0.031
<i>libycus</i>	y	0.009	-0.116	0.005	0.044	-0.155	0.024
<i>Pachyuromys</i>	x	0.028	0.085	0.009	0.043	0.114	0.015
<i>duprasi</i>	y	0.400	-0.120	0.013	0.044	-0.141	0.016
<i>Psammomys</i>	x	0.022	0.095	0.007	0.069	0.103	0.029
<i>obesus</i>	y	0.021	-0.131	0.008	0.081	-0.138	0.026

661

662 Table 2: Linear mixed effects model (LMER) analyses of the animal-to-background similarity. Similarity
 663 is measured as overlap of animal and background colour spaces (i.e. higher value indicates closer match
 664 to the background). LMER predicts the animal-to-background similarity in relation to focal vs. global
 665 background and desert rodent species. Rodent ID is included as random factor in the model.

Subject	Estimate	s.e.	DF	t-value	P
Similarity-to-background					
(Intercept) [°]	0.532	0.030	272.271	17.616	<0.001
Global background	0.155	0.032	156.102	4.801	<0.001
<i>Pachyuromys duprasi</i>	-0.046	0.065	263.176	-0.708	0.479
<i>Gerbillus gerbillus</i>	-0.013	0.042	285.692	-0.330	0.741
<i>Jaculus hirtipes</i>	-0.209	0.037	268.202	-5.556	<0.001
<i>Meriones libycus</i>	-0.245	0.099	261.733	-2.466	0.014
<i>Psammomys obesus</i>	0.171	0.065	263.176	2.618	0.009
<i>Gerbillus tarabuli</i>	0.104	0.041	266.876	2.514	0.012
Background * <i>duprasi</i>	-0.142	0.069	156.102	-2.049	0.042
Background * <i>gerbillus</i>	0.041	0.045	156.102	0.915	0.361
Background * <i>hirtipes</i>	-0.099	0.040	156.102	-2.472	0.014
Background * <i>libycus</i>	-0.077	0.105	156.102	-0.737	0.462
Background * <i>obesus</i>	-0.079	0.069	156.102	-1.143	0.254
Background * <i>tarabuli</i>	-0.076	0.044	156.102	-1.732	0.085

666 [°]Intercept includes factor level(s): Background [focal] & Species [*Gerbillus amoneus*].

667 Table 3: Tests of within-subject contrast results from repeated measures 3-ANOVA for background
 668 matching modelled through two vision systems: *vision* refers to predator vision system (mammalian or
 669 bird), *species* to the rodent species and *habitat* to background from where the animal was found from. In
 670 the chromatic match analysis results were similar if the full model was run with the 3-way-interaction.

Subject	Wilk's Λ	F	DF	Error	P
Luminance match					
Vision	0.996	0.479	1	132	0.490
Vision*Species	0.855	4.480	5	132	0.001***
Vision*Habitat	0.922	3.308	3	132	0.013**
Vis.*Hab.*Spec.	0.821	4.120	7	132	<0.001***
Chromatic match					
Vision	0.388	219.254	1	139	<0.001***
Vision*Species	0.843	5.194	5	139	<0.001***
Vision*Habitat	0.985	0.725	3	139	0.538

671